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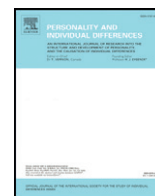
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Hans Eysenck's interface between the brain and personality: Modern evidence on the cognitive neuroscience of personality



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ABSTRACT

In this review, incorporating functional and structural MRI and DTI, with evidence gathered over the last 15 years, we examine the neural underpinnings of extraversion and neuroticism, the two major personality dimensions in Eysenck's (1967) biological model of personality. We present clear evidence that, as proposed by Eysenck nearly half-a-century ago, these traits relate meaningfully to the functioning and structure of various cortical and limbic brain regions. Specifically, there is a robust relationship between neuroticism and the functioning of several emotion processing networks in the brain, particularly during exposure to negative stimuli. The brain regions showing this association include a number of cortical regions implicated in emotion regulation, depression and anxiety, in addition to many sub-cortical/limbic regions. Currently, there are few studies directly assessing the relationship between extraversion and the cortical arousal system in the context of varying stimulations but data available so far are remarkably consistent with Eysenck's model. Future neuroimaging studies guided by relevant personality and cognitive theories, and with sufficient power to allow application of sophisticated analysis methods (for example, machine learning) are now needed to improve our understanding of the biological basis of individual differences and its application in the promotion of well-being and mental health.

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1. Introduction

Well before the advent of modern human brain imaging, Hans Eysenck, the visionary psychologist and the most influential personality researcher in recent history, proposed a theory (Eysenck, 1967) that went beyond description and measurement of personality and, for the first time, provided the neurophysiological causes of personality. It was unique in trying to explain extraversion and neuroticism, the two major personality dimensions in Eysenck's model (the third dimension, psychoticism, added formally later in 1975), in terms of individual differences in the functioning of aspects of the central nervous system (Eysenck, 1967). Here, we review neuroimaging evidence, gathered mainly over the last 15 years, examining the association between extraversion and/or neuroticism and brain activation/connectivity patterns elicited by a wide range of cognitive and affective tasks. We have included relevant functional magnetic resonance imaging (MRI), structural MRI and diffusion tensor imaging (DTI) studies generated in the context of Eysenck's three-factor model as well as Costa and McCrae's five-factor personality model (Neuroticism, Extraversion, Openness to

Experience, Agreeableness & Conscientiousness). There is a reasonable correspondence between the two models for extraversion and neuroticism (Costa & McCrae, 1995). We have also considered findings relating to the remaining three factors of the five-factor model as well as those relating to psychoticism, the third dimension in Eysenck's revised model (Eysenck & Eysenck, 1975), were examined within the same study, for completeness.

2. fMRI evidence

2.1. Cognitive processing

Eysenck's theory proposed that the extraversion–introversion dimension (extraversion = positive affectivity, marked by pronounced engagement with the external world and characterized by high sociability, talkativeness, energy and assertiveness) is caused by variability in cortical arousal (Eysenck, 1967). Those who score low for extraversion (introverts) have lower response thresholds and are consequently more cortically aroused than those who score high for extraversion (extraverts). It further postulated an inverted U-shaped relation between cognitive performance and 'level of arousal', jointly determined by environmental arousal potential (defined in terms of a range of environmental manipulations and task parameters) and subject arousability as reflected in

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extraversion. These postulates jointly predict that, at low environmental arousal potential, extraverts' performance would be lower than that of introverts'. As environmental arousal increases, performance of extraverts should improve and they should catch up with introverts; and, at high levels of environmental arousal, extraverts should out-perform introverts with a decline in introverts' performance, until it becomes so arousing as to evoke transmarginal inhibition (TMI) (Eysenck, 1994; Gray, 1964). With evocation of TMI, introverts may experience lower arousal increments than extraverts. There is considerable support for these predictions from behavioral studies (Eysenck, 1981). Eysenck's model further postulated that level of arousal, resulting from a combination of environmental arousal and subject arousability, is mediated by activity in a 'cortical arousal system', modulated by reticulo-thalamic-cortical pathways (Eysenck, 1967, 1981). A circuit that seemingly corresponds to this cortical arousal system, including the dorsolateral prefrontal cortex (dlPFC) and anterior cingulate regions, has been identified in studies applying fMRI to a wide range of cognitive tasks (Duncan & Owen, 2000). Importantly, findings of an fMRI study (Kumari, ffytche, Williams, & Gray, 2004), the only one so far to test the predictions concerning extraversion and cortical activity at different cognitive loads (or stimulation levels), are remarkably consistent with Eysenck's model. Specifically, this study showed that the higher the extraversion score, the greater the change in fMRI signal in the dlPFC and anterior cingulate from rest (through 1- and 2-back) to the 3-back working memory load condition. Furthermore, also consistent with Eysenck's model, which treats neuroticism and psychoticism dimensions as independent of extraversion, the relationship between extraversion and dlPFC and anterior cingulate activity was not found for neuroticism or psychoticism in Kumari et al.'s (2004) study.

Concerning neuroticism, Eysenck proposed that the neuroticism-stability dimension (neuroticism = negative affectivity, marked by emotional instability and low tolerance for stress or aversive stimuli, and characterized by anxiety, fear, moodiness, worry, envy, frustration, jealousy, and loneliness) is explained by differences in the level of activity primarily in the limbic system (Eysenck, 1967). Perhaps not surprisingly, most existing fMRI studies have examined the effects of neuroticism in implicit or explicit affect processing, emotion regulation, fear/anxiety stress induction paradigms (reviewed and discussed in the next section) rather than with pure cognitive paradigms. A very recent study, which examined the effects of personality using the five-factor model, found that decreased and increased effective connectivity within the working memory network, activated by a 3-back working memory task, were associated with high neuroticism and high conscientiousness, respectively (Dima, Friston, Stephan, & Frangou, 2015). Although these findings show a significant effect of personality in neuroplasticity, their interpretation is rather difficult because neuroticism and conscientiousness had opposite effects. The effects of conscientiousness, however, appear consistent with possible extraversion effects, since conscientiousness correlates positively with extraversion when assessed using the Eysenckian scales (Costa & McCrae, 1995). Notably, extraversion itself, as in the five-factor model, did not have any influence in this study.

An important line of enquiry in relation to fMRI of neuroticism using cognitive (and other) paradigms is indicated by experimental evidence showing greater trial-to-trial variability in cognitive performance (particularly reaction time) of high neuroticism scorers, relative to low neuroticism scorers (Robinson & Tamir, 2005). This behavioral effect may reflect task-irrelevant cognitions such as worries and preoccupations in neurotic individuals. Moment-to-moment brain signal variability is also known to be present in neuroimaging studies and has important implications for fMRI activation and connectivity studies (Garrett et al., 2013). Interestingly, moment-to-moment brain signal variability correlates with less, rather than more, reaction time variability across various paradigms and samples (Garrett, Kovacevic, McIntosh, & Grady, 2011; McIntosh, Kovacevic, & Itier, 2008; Misis, Mills, Taylor, & McIntosh, 2010; Raja Beharelle, Kovacevic, McIntosh, & Levine, 2012). Despite a highly likely influence of neuroticism in this phenomenon,

given its known association with reaction time variability, no published study has yet examined the effect of neuroticism in moment-to-moment/trial-to-trial variability in brain activations.

2.2. Affect

One of the great challenges faced by the human mind is the need to comprehend the content of other minds. Thus a rapidly increasing literature has sought to explore the psychological and neural mechanisms behind "the mental operations that underlie social interactions, including perceiving, interpreting, and generating responses to the intentions, dispositions, and behaviors of others" (Green et al., 2008), namely 'social cognition'. One of the most fundamental means we have of making these inferences is the emotion cues that other people display. However, individual differences associated with personality traits are a key influence on the way we perceive and respond to emotion cues (Britton, Ho, Taylor, & Liberzon, 2007). Indeed, our personality, whether we tend to be shy or outgoing, anxious or contented, has a major influence on our lives and the way we interact with the world around us (Hamann & Harenski, 2004). For example, highly neurotic individuals preferentially respond to negative emotion cues, and highly extravert individuals preferentially respond to positive emotion cues (Canli et al., 2001). Personality has these effects because it comprises an integrated pattern of thinking, feeling and behaving that varies between individuals but is relatively stable within individuals over time (Suslow et al., 2010). These chronic affective styles associated with personality tune the affective system to be more sensitive towards one class of cues than to another (Cunningham, Arbuckle, Jahn, Mowrer, & Abduljalil, 2010; Fruhholz, Prinz, & Herrmann, 2010). Beyond their everyday implications for understanding normal socio-cognitive behavior, neuroticism and extraversion are of great importance as trait dimensions, because of the implications for individual vulnerability for emotion-related psychopathologies such as anxiety and mood disorders (Brandes & Bienvenu, 2006; Foster & MacQueen, 2008; Gale et al., 2011; Keller, 2004; Klein, Kotov, & Bufferd, 2011; Wright, Kelsall, Sim, Clarke, & Creamer, 2013).

Adoption of cognitive neuroscience techniques undoubtedly facilitates a clearer understanding of how personality influences the way people react to emotion cues. It has even been said by some that neuroimaging might prove superior to behavioral or cognitive paradigms in characterising the effects of personality dimensions on reactivity to emotion cues (Harenski, Kim, & Hamann, 2009). The thinking here is that whereas behavioral and cognitive indices represent the combined effects of all brain activity components during a task, neuroimaging can isolate specific aspects of neural reactivity as being influenced by specific personality dimensions. Although some psychological determinants of individual variability in emotional reactivity have been determined at the behavioral level, research has only recently begun to explore the brain mechanisms that might enable this individual variability (Canli et al., 2001). This is because most prior neuroimaging studies have taken a group-based approach, in which the mechanism that determines emotional reactivity is studied in a group of healthy individuals not preselected for any specific criteria (Calder, Ewbank, & Passamonti, 2011; Hamann & Canli, 2004). Here the effect of individual differences on emotion perception at the neural level is frequently ignored or dismissed as statistical noise (Calder et al., 2011; Canli, 2004; Hamann & Canli, 2004). Yet these individual differences can exhibit remarkable stability within participants, suggesting that they are not random fluctuations, and that they relate to traits that are different between, but consistent within, individuals (Canli, 2004). With a correlational approach, individual differences in neural reactivity do not represent noise, rather they represent valuable signal that can reveal much about aspects of brain function of fundamental value to the study of social cognition (Canli & Amin, 2002; Hamann & Canli, 2004).

Since the trait of neuroticism involves enhanced processing of negative emotion cues (Canli et al., 2001), one way of establishing the

influence of neuroticism on patterns of brain activity is to study the neural response to *negative* emotions (Haas, Constable, & Canli, 2008). In the original study of neuroticism, extraversion and neural reactivity to emotion cues, Canli et al. observed that neuroticism correlated positively with neural reactivity to negative scenes in the middle frontal and temporal gyri, whilst extraversion correlated with reactivity to positive scenes in the inferior, middle and superior frontal gyri, the cingulate, the inferior and middle temporal gyri, the basal ganglia and amygdala (Canli et al., 2001). These correlations were both robust; and in the expected direction, that is greater neural reactivity to positive emotion cues was associated with high extraversion, whilst greater neural reactivity to negative emotion cues was associated with high neuroticism. Since this original study, subsequent research has confirmed and extended these findings in the visual modality, using symbols, faces or scenes. Thus, neuroticism has been associated with activity in the middle frontal gyrus ('negative' upsetting scenes) (Canli et al., 2001), medial PFC (sad faces) (Haas et al., 2008), anterior cingulate ('negative' upsetting scenes) (Haas, Omura, Constable, & Canli, 2007), temporal pole (sad faces) (Jimura, Konishi, & Miyashita, 2009), amygdala ('negative' upsetting scenes) (Cunningham et al., 2010; Harenski et al., 2009), and the basal ganglia ('negative' non-smiling/sad emotion symbols) (Bruhl, Viebke, Baumgartner, Kaffenberger, & Herwig, 2011), when perceiving facial emotion cues.

Beyond passive viewing of visual emotion cues or forced-choice labelling tasks, other research on personality and affective reactivity has sought to actively direct participant's view towards or away from emotion cues, by manipulating their attention. In this line of research, neuroticism has been shown to influence activity in brain regions such as the caudate and supramarginal gyrus even before a negative emotion cue is visible, that is through directing attention towards its mere anticipation (Bruhl et al., 2011), activation of the former having also been demonstrated more broadly for the anticipation of emotional music (Salimpoor, Benovoy, Larcher, Dagher, & Zatorre, 2011). Increasing the evaluative attentional processing demands by introducing emotion-related conflict has demonstrated that in such circumstances, neuroticism is typically associated with increased amygdala activity (Fruhholz et al., 2010), which makes sense given the role of the amygdala in vigilance (Davis & Whalen, 2001), and the aforementioned association of neuroticism with a predisposition towards negative emotion cues. Indeed, according to Eysenck's own biological theory of personality, high levels of neuroticism were hypothesized to reflect increased reactivity of the limbic system (of which the amygdala is part), which then predisposes highly neurotic people to react strongly to emotionally arousing experiences and take longer to return to pre-arousal states (Eysenck, 1967, 1994). Elsewhere in the limbic system, neuroticism has also been observed to associate with degree of activity in the medial PFC in response to emotional arousal, the authors in this study suggesting that neuroticism influences emotional reactivity by enhancing neural sensitivity to high levels of emotional arousal, predisposing highly neurotic individuals to react strongly to arousing experiences (Kehoe, Toomey, Balsters, & Bokde, 2012). Some emotion-relevant brain regions show increased or decreased activity in association with neuroticism depending upon specific emotional response/processes involved. For example, highly neurotic individuals show increased activity during anticipation of painful stimulation (possibly reflecting higher vigilance, anticipatory anxiety and emotional over-arousal) and decreased activity during painful stimulation (possibly reflecting emotional blunting, avoidance/passive coping strategy, learned helplessness, etc.) in the anterior cingulate, thalamus, parahippocampal gyrus and thalamus regions (Coen et al., 2011; Kumari et al., 2007).

In the temporal domain, evidence has shown that higher degrees of neuroticism are associated with a sustained haemodynamic response across time in the medial PFC to negative stimuli, not just with an instantaneous response (Haas et al., 2008). Such a link might thereby create a mechanism whereby rumination over time could facilitate the association of neuroticism with increased vulnerability for depression.

The importance of taking temporal dynamics into account when using neuroimaging to study the influence of personality on affective reactivity is further underscored when distinguishing between initial reactivity to an emotional stimulus, and subsequent recovery once an emotion cue terminates or ceases to be relevant. Closer examination of the time course of neural response in the amygdala in one study demonstrated that whilst initial amygdala reactivity did not predict trait neuroticism, slower amygdala recovery from negative images after their offset did predict greater neuroticism (Schuyler et al., 2012). Because neuroticism is associated with greater perseveration of emotional events (Robinson, Wilkowski, Kirkeby, & Meier, 2006), this link between greater neuroticism and slower amygdala recovery might form the basis of the inability to alter negative mood state once established, thereby enabling another important element of the increased vulnerability for depression associated with neuroticism.

Following the same logic as for neuroticism, one way of establishing the influence of extraversion on patterns of brain activity is to study the neural response to *positive* emotions. Thus a high degree of extraversion has been linked in this way with a greater response to positive visual emotion cues e.g., happiness, in the amygdala (Suslow et al., 2010), the basal ganglia (Canli et al., 2001), and anterior cingulate cortex (Canli, Amin, Haas, Omura, & Constable, 2004; Canli, Sivers, Whitfield, Gotlib, & Gabrieli, 2002; Haas, Omura, Amin, Constable, & Canli, 2006). These brain regions are all known for their generic roles in emotion perception (Etkin, Egner, & Kalisch, 2011; Kringelbach & Berridge, 2009; Phan, Wager, Taylor, & Liberzon, 2002; Phillips, Drevets, Rauch, & Lane, 2003; Sabatinelli et al., 2011). Functional connectivity between the anterior cingulate and inferior parietal lobule, middle frontal gyrus and right orbitofrontal gyrus may also increase with degree of extraversion during reactivity to positive emotion cues (Haas et al., 2006), which is consistent with the known functional neuroanatomy of this region (Bush, Luu, & Posner, 2000), and likely reflects increased attentional input to monitoring for positive emotion cues among other functions (Ptak, 2012; Vandenberghe & Gillebert, 2009).

Subcortical regions such as the thalamus have also been implicated as enabling the influence of extraversion on the neural response during (anticipation of) positive emotion cues (Bruhl et al., 2011). In the context of the protective influence of high extraversion on psychological well-being (Abbott et al., 2008), a relationship with emotional reactivity in such a deep brain structure might be particularly difficult to modify in people with low extraversion, for example by psychotherapy (Wang et al., 2013). Beyond the confines of the supposed link between extraversion and positive emotional reactivity, other research suggests that extraversion in fact reflects a generic increase in social engagement irrespective of emotional valence (Ponari, Trojano, Grossi, & Conson, 2013). Along these lines, one study demonstrated a link between emotional reactivity in the fusiform gyrus to both positive and negative emotion cues in an attentional dot-probe task (Amin, Constable, & Canli, 2004), which would be consistent with that region's known role as an alerting mechanism to emotional content in social communications (Schindler, Wegrzyn, Steppacher, & Kissler, 2015).

Historically, literature on the relationship between personality traits and emotion perception mechanisms has focused on visual cues, yet beyond facial cues, another crucial means of transmitting emotion cues is through prosody. By manipulating features of speech such as pitch, duration, loudness, voice quality and spectral properties (Ross, 1993), we can alter our tone of voice and thereby alter the emotion that we convey. It is an especially effective means of conveying emotional meaning in everyday contexts (Scherer, 1986), because the ability to produce, coordinate, and understand emotion signals in speech in this way is a prerequisite for fundamental attributes of social cognition including, 'negotiating claims to power, respect, or equality, defining degrees of intimacy, showing affiliation or non-affiliation, avoiding threats, repairing interpersonal misunderstandings and so forth' (Arndt & Janney, 1991). Indeed, in some situations, it may be the only means of expressing nonverbal emotion cues. Thus far, there

has been only one prior report on the effect of individual differences in personality on the neural response to prosodic emotion cues (Bruck, Kreifelts, Kaza, Lotze, & Wildgruber, 2011). In this study, for explicit emotional prosody identification relative to control tasks (task driven activity), positive correlations were observed between neuroticism and neural responsivity in the amygdala and anterior cingulate. During prosody identification for emotional vs. neutral trials (stimulus-driven activity), a correlation was observed with the neural response in medial frontal cortex, to happy prosody. Perhaps reflecting the clearer trends for neuroticism-linked than for extraversion-linked patterns of emotional reactivity with visual emotion cues, no correlations were observed between brain activity patterns and extraversion for prosodic cues in this study.

Overall, there is no doubt that existing studies provide strong support for a brain basis of individual differences in extraversion and neuroticism, and the findings of many of these studies, despite them not being specifically formulated to test (in fact many conducted in a theoretical vacuum), can be considered broadly in line with Eysenckian predictions.

3. Structural MRI

That personality is biologically-based as proposed by Eysenck immediately becomes apparent when considering evidence from structural MRI. One particular overview study was able to demonstrate associations with the volume of different brain regions and four out of the 'big five' personality traits (DeYoung et al., 2010). Specifically, extraversion covaried with volume of medial orbitofrontal cortex, a brain region involved in processing reward information (Noonan, Kolling, Walton, & Rushworth, 2012). Neuroticism covaried with the volume of brain regions associated with threat, punishment, and negative affect, such as the dorsomedial PFC and portions of the left medial temporal lobe (Kalisch & Gerlicher, 2014; Strange & Dolan, 2006). However, greater levels of neuroticism have also been linked to reduced overall ratio of brain to intracranial volume across the brain as a whole, particularly the element of neuroticism relating to chronic experience of arousing negative emotions (Knutson, Momenan, Rawlings, Fong, & Hommer, 2001), which might possibly reflect the cumulative effects of stress reactivity (McEwen, 2006). Agreeableness (which correlates negatively with Psychoticism; Costa & McCrae, 1995) in the DeYoung study, covaried with volume in regions that process information about the intentions and mental states of other individuals, including the posterior cingulate cortex and superior temporal gyrus (Nummenmaa & Calder, 2009; Schlaffke et al., 2015). Finally, conscientiousness covaried with volume in lateral PFC in the De Young study, a region involved in planning and the voluntary control of behavior (Tanji & Hoshi, 2008). Often the seat of functional associations with personality (see Section 5), the PFC cortex may further exhibit separable patterns of association dependent on the particular personality trait in question. Specifically, extravert people may have a thinner layer of cortical gray matter ribbon in regions of the right inferior PFC and fusiform gyrus, compared to introvert people, whereas neurotic people may have a thinner cortex mantle in anterior regions of the left orbitofrontal cortex (Wright et al., 2006). The difference in hemispheric lateralization for these effects was significant in this study, perhaps reflecting literature that greater left-sided activity of the PFC has classically been associated with positive affect as found in extraversion, whereas greater right-sided PFC activity has classically been associated with negative affect as found in neuroticism (Davidson, 2003; Spielberg, Stewart, Levin, Miller, & Heller, 2008).

Perhaps the greatest body of research on the structural bases of the five major personality traits has come from Voxel-Based Morphometry (VBM), a technique with two distinct advantages relative to traditional tracing methods. Firstly, it allows detection of subtle morphometric differences in brain structure that may not be discernible by visual inspection, and secondly, it allows investigation of the entire brain rather than a particular structure, in an automatic and objective manner (Scarpazza,

Tognin, Frisciata, Sartori, & Mechelli, 2015). In the body of research using VBM to examine personality-related differences, one major area of focus has been the amygdala. In one of the early studies, neuroticism appeared to negatively correlate with gray matter density in the right amygdala, whereas extraversion was positively correlated with gray matter density in the left amygdala (Omura, Todd Constable, & Canli, 2005). Given what we know about the affective style of extraversion and neuroticism, this laterality pattern would again be consistent with a model of affect that posits left-lateralized hemispheric specialization for positive affect or approach-oriented behavior, and right-lateralized hemispheric specialization for negative affect or withdrawal-oriented behavior (Maxwell & Davidson, 2007; Shackman, McMenamin, Maxwell, Greischar, & Davidson, 2009). However, subsequent research has not confirmed these results for neuroticism. In later literature, correlations with neuroticism have either been positively rather than negatively correlated, and the foci of the volumetric correlation has concerned the left/bilateral rather than right amygdala (Koelsch, Skouras, & Jentschke, 2013; Mincic, 2015). Nevertheless, amygdala volume differences in one form or another might therefore be indicative of an individual's risk of depression (Whittle et al., 2014), which would certainly fit with this structure's role in detecting emotional saliency and social relevance (Adolphs, 2008, 2010; Murray, Brosch, & Sander, 2014). Other gray matter volume differences reportedly linked to degree of neuroticism have included increased volume in the cerebellum, and decreased volume in the superior frontal gyrus (Lu et al., 2014), which have been linked to negative affect coordination and regulation of negative emotions respectively (Baumann & Mattingley, 2012; Becker & Stoodley, 2013; Falquez et al., 2014; Mak, Hu, Zhang, Xiao, & Lee, 2009; Mothersill, Knee-Zaska, & Donohoe, 2016). As a whole, this body of evidence suggests that neuroticism is related to several brain regions involved in regulating negative emotions.

Regarding extraversion, the major finding seems to concern personality-dependent volume differences in the orbitofrontal cortex and other PFC brain regions. Thus increasing extraversion appears to correlate positively with increased/decreased orbitofrontal cortex gray matter density/volume (Coutinho, Sampaio, Ferreira, Soares, & Goncalves, 2013; Cremers et al., 2010; Omura et al., 2005). As mentioned above, changes in amygdala volume or density have also been observed to depend on the degree of extraversion an individual exhibits (Cremers et al., 2010; Lu et al., 2014; Omura et al., 2005). Given that extraversion acts as a protective factor against development of anxiety disorders and depression, one possible explanation is that the reduced likelihood of highly extravert individuals developing an affective disorder relates to modulation of emotion processing through the orbitofrontal cortex and the amygdala, two structures often implicated in concert in patients with diagnoses of affective disorders (Blackmon et al., 2011; Kanske, Heissler, Schonfelder, & Wessa, 2012; Zald et al., 2014; Zhang et al., 2014). Other frontal lobe structures which have evidenced a relationship between extraversion and personality-dependent changes in gray matter density or volume have included the anterior cingulate cortex, inferior frontal gyrus, middle frontal gyrus, superior frontal gyrus, all of which are known to be involved in emotional and socio-cognitive processes (Coutinho et al., 2013; Cremers et al., 2010; Forsman, de Manzano, Karabanov, Madison, & Ullen, 2012; Lu et al., 2014). Taken as a whole, the structural evidence from VBM suggests that one aspect of personality differences may be individual variation in the organization of brain networks for evaluation of socially relevant stimuli, including regions involved in recognition of social-affective stimuli and social judgment.

4. Connectivity

Whilst the evidence presented in the previous sections has revealed important initial insights into the structural and functional neural correlates of personality, current knowledge of relationships between brain function and structures and personality traits is still rather limited.

White matter mediates communications in the brain and is critical for the integrity of brain function. As noted above, neuroticism indexes the tendency to experience negative affect, and functional imaging has evidenced the importance of the relationship between functioning of the amygdala and PFC in response to negative emotion cues (Haas et al., 2007; Harenski et al., 2009; Hooker, Verosky, Miyakawa, Knight, & D'Esposito, 2008). It is perhaps not surprising therefore that subsequent research with Diffusion Tensor Imaging (DTI) has evidenced a positive correlation between neuroticism and a measure of loss of white matter integrity in the anterior cingulum and uncinate fasciculus, tracts that connect the PFC and amygdala (Xu & Potenza, 2012). This modulatory effect of neuroticism on the connectivity of the PFC and amygdala is in line with similar demonstrations with functional MRI measures in the context of affective reactivity (Cremers et al., 2010). However, other DTI evidence has suggested that the breakdown in white matter integrity associated with neuroticism may be more widespread, and include fibres connecting frontal, occipital, parietal and temporal lobes, tracts connecting orbitofrontal regions with limbic regions, fibre tracts connecting thalamic nuclei with the frontal lobes, and cross-hemispheric pathways including the corpus callosum (Bjornebekk et al., 2013). It was speculated by the authors that the more widespread relationship between neuroticism and white matter integrity observed in this second study might reflect its greater methodological sensitivity. The wide distribution of effects in the latter study further suggests that general rather than regionally specific processes might be driving the effects, and emphasizes the importance of collecting white matter integrity measures throughout the brain.

Evidence for personality-linked patterns of functional connectivity independent of performance of a given task, comes from the analysis of resting state data, that is from the patterns of spontaneous activity observed, that are intrinsic and stable across time. Identifying brain correlates of a situation-independent personality structure requires evidence of a stable 'default' mode of brain functioning (Sampaio, Soares, Coutinho, Sousa, & Goncalves, 2014). Thus in terms of low-frequency fluctuations, neuroticism has been observed to correlate negatively with regional activity of the middle frontal gyrus and precuneus, whilst extraversion has been observed to correlate positively with regional activity of the striatum, precuneus and superior frontal gyrus (Kuniso et al., 2011). The former might reflect the association of neuroticism with the role of the precuneus in anticipatory fear (Kumari et al., 2007), and an inbuilt mechanism to attempt emotional regulation in order to deal with the predisposition to negative affectivity (Pan et al., 2014; Seo et al., 2014). For extraversion, the striatal correlation observed more likely reflects the importance of reward processing (Schultz, 2015), but the positive involvement of the precuneus may this time reflect a reduced need for emotion regulation. The link between low frequency oscillations in the precuneus in the resting state and degree of extraversion has subsequently been confirmed by another group (Wei et al., 2014).

Seed-based correlation analysis has continued this theme of differences between neuroticism and extraversion in reward processing and need for socio-emotional regulation. Thus higher neuroticism scores have been observed to correlate with increased amygdala resting state functional connectivity with the precuneus, and decreased amygdala resting state functional connectivity with the temporal poles, insula, and superior temporal gyrus (Aghajani et al., 2014). Conversely, higher extraversion scores in this study correlated with increased amygdala resting state functional connectivity with the putamen, temporal pole, insula, and occipital cortex. These changes in amygdala resting state functional connectivity associated with neuroticism perhaps reflecting the less adaptive perception and processing of self-relevant and socio-emotional information frequently seen in neurotic individuals (Robinson, Moeller, & Fetterman, 2010), whereas the amygdala resting state functional connectivity pattern associated with extraversion perhaps reflecting the heightened reward sensitivity and enhanced socio-emotional functioning in extraverts. Placing the seed region in the

precuneus or anterior cingulate has revealed that neuroticism predicts resting state functional connectivity with brain areas involved in self-evaluation and fear, whilst extraversion predicts resting state functional connectivity with brain areas involved in reward and motivation (Adelstein et al., 2011). Given that neuroticism is known to be associated with anxiety and self-consciousness (Montag, Reuter, Jurkiewicz, Markett, & Panksepp, 2013), and extraversion is implicated in gregariousness and excitement-seeking (Li et al., 2010), it seems that the major contribution of this literature is the clear consistency it evidences with known qualities about each personality domain.

At a more general level, compared with less neurotic individuals, highly neurotic individuals may exhibit a whole-brain network structure resembling more of a random network, with weaker functional connections. In such highly neurotic individuals, Servaas et al. (2015) demonstrated that functional sub-networks could be delineated less clearly and the majority of these showed lower efficiency. The authors concluded that the 'neurotic brain' has a less than optimal functional network organization and that it shows signs of functional disconnection. Moreover, in high compared with low neurotic individuals, emotion and salience sub-networks seemed to have a more prominent role in the information exchange relative to the sensorimotor and cognitive control sub-networks (Servaas et al., 2015).

5. Future directions: What might Eysenck have wanted for the future?

If we could go back to the 1990s, the easiest way to answer this question would have required going to the canteen of the Institute of Psychiatry (now known as the Institute of Psychiatry, Psychology and Neuroscience) around 10.30 am and approach Hans Eysenck. We believe he would have given insightful suggestions with a smile, just as he did when approached by the second author when she first arrived, an unknown hopeful post-doc from India, at the Institute of Psychiatry. Nonetheless, we identify some areas, which we believe will advance our understanding of the neural basis of individual differences.

We believe that there is a great need to understand why some people are better at interpreting emotion cues than others, and we believe that personality effects are one such mechanism by which these individual differences occur. If we are able to demonstrate clear personality-linked differences in the way people's brains shape their response to emotion cues, a myriad of future applications will likely ensue (Bruck, Kreifelts, & Wildgruber, 2011). Can brain activation patterns be used to classify normal and dysfunctional emotional reactivity with machine learning classifiers? Can we distinguish the types of people (i.e., personality types) skilled in decoding nonverbal emotion cues from those with difficulties interpreting such cues based on typical patterns of brain activation? Pursuing an individual differences approach in the study of emotional reactivity not only holds the potential to further advance current models of social cognition; it may also guide the way to a better understanding of individual disturbances of emotion perception associated with psychiatric disorders. Here it is worth noting that in the latest incarnation of current diagnostic guidelines (*Diagnostic and Statistical Manual of Mental Disorders*; DSM-V), there is much greater emphasis on dimensional approaches to describing mental ill health than in previous editions (Kraemer, 2007). From a clinical perspective, a clear demonstration of a relationship between personality and emotional reactivity could be used to argue that changes in emotion perception could be harnessed as a reasonable alternative way of monitoring clinical improvement among individuals receiving treatment for personality disorders, as a 'surrogate marker'. Pursuing other cognitive and affective functions which relate to individual differences in behavioral studies (but not considered so far by personality neuroscience researchers), and also found to be aberrant in certain psychiatric disorders, would be just as valuable.

We suggest that future studies are also sufficiently powered to examine personality effects, in particular trait interactions (e.g., extraversion

with/without high neuroticism), in brain responses at rest, to varying cognitive demands and emotional challenges, and rule out the influence of other factors such as gender, age and IQ (which also affect brain properties). Most existing studies of extraversion, neuroticism (reviewed earlier) and related traits (reviewed by McNaughton, Corr, & DeYoung, 2015) have been too small to examine such effects and mostly ignored them. It may be possible to achieve larger samples sizes with increased co-operation between research groups, without much additional cost (Mar, Spreng, & Deyoung, 2013). We further suggest that personality neuroscience researchers, wherever possible, utilize relevant personality theories (e.g., reinforcement sensitivity theory) (Corr, 2008) and cognitive psychology (e.g., to determine task properties, cognitive processes involved, time on task etc.) to guide their neuroimaging experiments and interpretations. Finally, we suggest that future studies should examine the influence of personality traits in trial-to-trial variability in brain signals. If confirmed, personality influences in these signals have implications for our understanding of brain basis of individual differences in personality but also for the neuroimaging community at large.

6. Conclusions

The findings reviewed above provide compelling support that, as proposed by Eysenck, individual differences in extraversion and neuroticism are related to the functioning and structure of various brain regions. Our review suggests a strong relationship between neuroticism and emotion processing neural networks, particularly during exposure to negative emotion cues, and suggests a relationship between some of the same emotion processing regions and extraversion in response to positive emotion cues. These regions include some cortical regions implicated in emotion regulation, depression and anxiety, in addition to most sub-cortical/limbic regions. At present, there are few data directly assessing the relationship between extraversion and cortical arousal system in the context of varying stimulation levels (e.g., by increasing cognitive load), but they are remarkably consistent with Eysenck's model.

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